# The Ecology of Pelagic Amphipoda, II

## Observations on the Reproductive Cycles of Several Pelagic Amphipods from the Waters off Southern California

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The purpose of this study was to utilize midwater samples from off the coast of southern California to determine the general patterns of the reproductive cycles of the local pelagic Amphipoda. All of the materials analyzed during this project were collected in the area of the Outer Santa Barbara Passage at approximately 33°20′N, 118°40′W. All samples were collected with an Issacs-Kidd Midwater Trawl (Issacs and Kidd, 1953) from the R/V "Velero IV" of the Allan Hancock Foundation, University of Southern California. Partial support for this work was furnished by National Science Foundation Grants (G10691 and G23467).

Complete information on the reproductive cycles of amphipods is scarce and, in the case of pelagic species, difficult to obtain. Some data can be gained from various expedition reports in which the presence of ova and young in the brood pouches is recorded. Some of these past records are mentioned in this paper.

### Methods and Materials

Samples were taken at various depths and at different times of the day and night from the summer of 1962 through the spring of 1963 using a 10 × 10-ft Issacs-Kidd Midwater Trawl. A few samples were used from later in 1963 for qualitative confirmation of the data gathered earlier. Species accounts and analyses of vertical distributions and migrations are presented by Brusca (1967).

For comparative information on fluctuations in population densities throughout the year, counts made from pint aliquots were converted to the number of individuals captured per hour trawling time. Such values are only approximate and do not account for the suspected gregarious nature of these pelagic amphipods, but they probably do reflect the general trends in the population size. Complete raw data are on file with the author.

### Observations

Presented in this section are only those data which specifically pertain to the reproductive cycles of these animals. For a more detailed species account and reference lists see Brusca (1967).

#### Suborder Gammaridea

#### Family Eusiridae

*Rhachotropis natator* (Holmes)

A total of 77 specimens was taken from pint aliquots. None of these individuals was noted to be carrying ova or young in the brood pouches, but there was some variation in the size range and in the density of the population. Table 1 illustrates these changes.

Since a rise in population density accompanied an extension of the lower limit of the size range during the winter months, this time probably represents the entrance of young into the adult or "catchable" population. The data

TABLE 1

Seasonal Changes in Size Range (SR), and Average Number per Trawl Hour (n/th) Based on Positive Samples for *Rhachotropis natator*

| Season | SR (mm) | n/th |
|---|---|---|
| Summer | 20 (1 spec) | 4 |
| Fall | 13–17 | 22 |
| Winter | 9–16 | 32 |
| Spring | 9–17 | 24 |

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are too scant, however, to draw any definite conclusions.

### Family LYSIANASSIDAE

*Paracallisoma coecus* (Holmes)

During this study 56 specimens were recovered from pint aliquots. The presence of ovigerous females was noted in October and November and a few were carrying young in May. Seasonal variations in number and size offer no conclusive data due to the small quantity of individuals collected.

*Cyphocaris anonyx* Boeck

A total of 115 individuals was collected from pint aliquots. Ovigerous females were noted during the months of May, June, July, and August, indicating that this season is a time of high reproductive activity. No females were found which were carrying young. As shown in Table 2, there was an extension of the lower limit of the size range during the summer months and an increase in population density, probably indicating the entrance of young into the mature population. The drop in mean size in the fall may reflect the death of the older portion of the population.

*Cyphocaris richardi* Chevreux

A total of 193 specimens was sorted from pint aliquots. Table 3 illustrates the pertinent reproductive information.

As can be seen, the greatest production of eggs occurred during the fall months, and young were present in the brood pouches only in the winter. Males were most abundant at the times of high ova production. It appears that embryonic development took place throughout the winter months, with the release of young completed by early spring.

There was a slight drop in mean size and in the lower limit of the size range in the spring, followed by a more drastic decrease in these measurements during the summer. These periods indicate the time of the entrance of young into the adult population.

TABLE 2

SEASONAL VARIATION IN MEAN SIZE (MS), SIZE RANGE (SR), AND AVERAGE NUMBER PER TRAWL HOUR (n/th) FOR *Cyphocaris anonyx*

| SEASON | MS(mm) | SR(mm) | n/th |
|---|---|---|---|
| Summer | 11.5 | 4–14 | 37 |
| Fall | 8 | 6–12 | 4 |
| Winter | 13.5 | 5–15 | 13 |
| Spring | 10 | 7.5–13.5 | 30 |

### Suborder HYPERIIDEA

### Family PLATYSCELIDAE

*Platyscelus serratulus* Stebbing

Only 8 specimens of this species were taken, all of which were females. Although Hurley (1956) collected *P. serratulus* from southern California waters during the months of January and February, the individuals captured during this present study were taken in September and November. Ovigerous females were noted in November. Sizes ranged from 3 to 7 mm with a mean of 5.1 mm for the 8 specimens collected.

### Family PRONOIDEA

*Eupronoe minuta* Claus

In all, 322 individuals were collected from pint aliquots. From the data presented in Table 4 it can be seen that some of the reproductive activity of *E. minuta* is not clear, in that the greatest production of ova occurred at the same time as the highest incidence of young in the brood pouches. Apparently young were released from the females early in the fall. This release is indicated by a drop in the percentage of females carrying young, a drop in mean size, and an extension of the lower limit of the size range. Males were present only during the fall months, suggesting that that was the period of fertilization.

### Family PHROSINIDAE

*Primno macropa* Guerin

A total of 315 individuals was taken from pint aliquots. The pertinent reproductive data are recorded in Table 5.

Maximum production of eggs occurred in the

TABLE 3

Seasonal Variations in the Percentages of Mature Females Carrying Ova (O), Carrying Young (Y), Mean Size (MS), Size Range (SR), Female/Male Ratio (f/m), and the Average Number per Trawl Hour (n/th) Based on Positive Samples for *Cyphocaris richardi*

| season | O | Y | MS(mm) | SR(mm) | f/m | n/th |
|---|---|---|---|---|---|---|
| Summer | 10% | 0% | 20 | 11–29 | 1.5/1 | 33 |
| Fall | 43% | 0% | 22 | 17–28 | 0.7/1 | 56 |
| Winter | 10% | 13% | 26 | 18–33 | 1/1 | 51 |
| Spring | 14% | 0% | 24 | 15–30 | 1.6/1 | 48 |

TABLE 4

Seasonal Variation in the Percentages of Mature Females Carrying Ova (O) and Young (Y), Mean Size (MS), and Size Range (SR), and Average Number per Trawl Hour (n/th) for *Eupronoe minuta*

| season | O | Y | MS(mm) | SR(mm) | n/th |
|---|---|---|---|---|---|
| Summer | 35% | 15% | 6 | 4.2–7.8 | 4 |
| Fall | 26% | 0% | 5.5 | 3–7.5 | 26 |
| Winter | 10% | 0% | 5.5 | 3.5–7.5 | 8 |
| Spring | 25% | 15% | 5.7 | 5–7 | 5 |

TABLE 5

Seasonal Variation in the Percentages of Mature Females Carrying Ova (O), and Young (Y), Mean Size of Females (MSf), and Males (MSm), Size Range of Females (SRf), and Males (SRm), and Average Number per Trawl Hour (n/th) for *Primno macropa*

| season | O | Y | MSf | MSm | SRf(mm) | SRm(mm) | n/th |
|---|---|---|---|---|---|---|---|
| Summer | 50% | 5% | 7 | 5 | 4–12 | 4–9 | 5 |
| Fall | 50% | 3% | 8.5 | 4.5 | 4–12 | 4–5 | 26 |
| Winter | 33% | 0% | 7 | none | 5–13 | none | 4 |
| Spring | 27% | 25% | 12 | none | 6–14 | none | 4 |

summer and fall months, with a high percentage of the females carrying young by spring. Males were captured only during times of highest ova production. The young were released into the adult population during the summer, as indicated by a drop in mean size, an extension of the lower limit of the size range, and an increase in the average number per trawl hour by the fall months.

### Family Cystisomidae

*Cystisoma fabricii* Stebbing

Only 31 specimens were collected. Ovigerous females were noted in October and December, and some were carrying young during January and August. There was an increase in the number of males collected at times of ova production. Because of the paucity of specimens no definite conclusions can be drawn.

*Cystisoma pellucidum* (Suhn)

Only 4 individuals were collected during the entire study period, including a single ovigerous female in July (64 mm). Other specimens were taken in August (male, 70 mm), January (male, 116 mm), and May (damaged, 70 mm).

### Family Oxycephalidae

*Calamorhynchus pellucidus* Streets

A single male specimen (19 mm) was collected during September. Fage (1960) gave an account of the known reproductive biology of

this species in his monograph on the oxycephalids.

*Oxycephalus clausi* Bovallius

Only two individuals of this species were taken (September: female, 30 mm; and January: female, 25 mm). Neither of these specimens was carrying ova or young. Again, Fage (1960) discussed the reproductive biology of *O. clausi.*

*Streetsia challengeri* Stebbing

This species was by far the most common oxycephalid taken during this study; 67 specimens were collected from pint aliquots. Table 6 gives information regarding breeding activity.

Egg production was highest in the spring, at which time the ratio of females to males was lowest. Young were most prevalent in the brood pouches during the fall. They were probably released from the parents in late fall and early winter, as indicated by a drop in mean size during the fall. The winter size data do not correlate with the suggested time of the entrance of young into the adult population. Fage (1960) reviewed some of the reproductive biology of this species.

Family HYPERIIDAE

*Hyperia spinigera* Bovallius

It has been suggested by Shoemaker (1945) that *Hyperia spinigera* may be conspecific with *H. galba.*

Only six specimens of this species, all males, were collected throughout this study. The months of capture and sizes of individuals were as follows: August: 1 male (5 mm); September: 1 male (4 mm); October: 3 males (4,5, 15 mm); November: 1 male (4 mm).

The presence of this species during only the late summer and early fall may have some bearing on the reproductive activity, but paucity of individuals prevents speculation.

*Hyperia bengalensis* (Giles)

A total of 52 individuals was sorted from pint aliquots. Specimens were captured only during the months of August through November. During this time the mean size of the female population increased from 2 mm to 2.8 mm, and the size range for females increased from 2–2.4 mm to 1.7–3.5 mm. Males were taken only in September, October, and November, and were consistently larger than the females displaying a mean size of 3.3 mm and a size range of from 3 to 4 mm. The ratios of females to males for these three months were 5/1, 15/1, and 3/1, respectively.

Egg production was highest in September, with about 40% of the females being gravid; values of less than 20% were noted for the other three months. The percentages of females carrying young in the brood pouches increased throughout the four months during which *H. bengalensis* was captured (August, 0%; September, 10%; October, 15%; November, 45%).

The reasons underlying the odd and sudden appearance and disappearance of this species from the local population are unclear and consequently the breeding cycle is incomplete.

*Hyperia galba* (Montague)

A total of 178 specimens was collected from pint aliquots. Table 7 summarizes the reproduc-

TABLE 6

SEASONAL VARIATION IN THE PERCENTAGES OF MATURE FEMALES CARRYING OVA (O) AND YOUNG (Y), MEAN SIZE OF FEMALES (MSf) AND MALES (MSm), SIZE RANGE OF FEMALES (SRf), AND MALES (SRm), FEMALE/MALE RATIO (f/m), AND AVERAGE NUMBER PER TRAWL HOUR (n/th) FOR *Streetsia challengeri*

| SEASON | O | Y | MSf (mm) | MSm (mm) | SRf (mm) | SRm (mm) | f/m | n/th |
|---|---|---|---|---|---|---|---|---|
| Summer | 20% | 30% | 21.5 | 22 | 13–27 | 20–24 | 8/1 | 2 |
| Fall | 0% | 40% | 14 | 15.5 | 7.5–26 | 14–17 | 11/1 | 2 |
| Winter | 0% | 0% | 22 | 13 | 21–22.5 | 11.5–14 | 2/1 | less than 1 |
| Spring | 51% | 0% | 19 | 14 | 12–23 | 11.5–16 | 3/1 | 2 |

TABLE 7

Seasonal Variation in the Percentages of Mature Females Carrying Ova (O) and Young (Y), Mean Size of Females (MSf) and Males (MSm), Size Range of Females (SRf) and Males (SRm), and the Female/Male Ratio (f/m) of *Hyperia galba*

| season | O | Y | MSf(mm) | MSm(mm) | SRf(mm) | SRm(mm) | f/m |
|---|---|---|---|---|---|---|---|
| Summer | 0% | 45% | 9 | 12 | 8–12.5 | 11–13 | 4.5/1 |
| Fall | 10% | 17% | 9 | 11.5 | 6–19.5 | 9–15 | 4.6/1 |
| Winter | 50% | 18% | 10.5 | 10.5 | 7.5–12.5 | 6–15 | 1.5/1 |
| Spring | 98% | 0% | 9 | 11.5 | 8.5–10 | 8.5–17 | 1.5/1 |

tive information. Egg production was highest in the summer months, and the highest incidence of young in the brood pouches was in the spring. The abundance of males does not appear to correlate with the presence of ova. Young were released from the parents by summer, but their entrance into the mature population was not reflected in the size data until fall, at which time there was an extension of the lower limit of the size ranges for both males and females. This suggestion is also supported by an increase in population density from an average of 3 individuals per trawl hour in the summer to 10 per trawl hour during the fall months. There appears to be about a three-months' lag between the release of young from the brood pouches and their entrance into the catchable population. The whereabouts of the newborn amphipods is unknown. Analyses of local plankton samples taken during the suspected time of release offered no positive information.

## Family VIBILIIDAE

### *Vibilia armata* Bovallius

A total of 2,742 individuals was sorted from pint aliquots. Some of the reproductive data for this species are difficult to interpret. Stephensen (1918) reported on collections from the Mediterranean in which he found breeding females in January and February and from June through September and young at all times of the year. In this present study no ovigerous females were noted during the winter and only a low percentage was recorded for the rest of the year (Table 8). The presence of young in the brood pouches suggests that the release from the parents took place in the late spring and early summer, at which time an extension of the lower limit of the size range and a drop in mean size were noted. The population density, however, did not show a significant increase until early fall.

### *Vibilia viatrix* Bovallius

In all 658 individuals were recorded from the sorting of pint aliquots. Stephensen (1918) reported specimens of *V. viatrix* in breeding condition during March and October in the North Atlantic. The information gathered in this present study is given in Table 9.

Ovigerous females were most abundant in the fall and a high percentage was carrying young by winter. Apparently juveniles were released from the brood pouches during the

TABLE 8

Seasonal Variation in the Percentages of Mature Individuals Carrying Ova (O) and Young (Y), Mean Size (MS), Size Range (SR), and Average Number per Trawl Hour (n/th) for *Vibilia armata*

| season | O | Y | MS(mm) | SR(mm) | n/th |
|---|---|---|---|---|---|
| Summer | 3% | 10% | 6.5 | 3–10 | 14 |
| Fall | 8% | 35% | 7.5 | 6–10 | 251 |
| Winter | 0% | 45% | 7 | 6–9 | 71 |
| Spring | 8% | 51% | 8.5 | 6–10 | 30 |

TABLE 9

SEASONAL VARIATION IN THE PERCENTAGES OF MATURE INDIVIDUALS CARRYING OVA (O) AND YOUNG (Y), MEAN SIZE (MS) AND SIZE RANGE (SR), AND AVERAGE NUMBER PER TRAWL HOUR (n/th) FOR *Vibilia viatrix*

| SEASON | O | Y | MS(mm) | SR(mm) | n/th |
|---|---|---|---|---|---|
| Summer | 12% | 25% | 9 | 4–15.5 | 38 |
| Fall | 20% | 40% | 9 | 7–12 | 8 |
| Winter | 9% | 60% | 10.5 | 7–14 | 5 |
| Spring | 3% | 21% | 11.5 | 8.5–15 | 3 |

spring and summer months, as is shown by a drop in mean size and an extension of the lower limit of the size range along with an increase in the average number per trawl hour. All of these indications became obvious during the summer.

## Family PHRONIMIDAE

### *Phronima sedentaria* (Forskål)

A total of 575 individuals was sorted from pint aliquots. Previously reported reproductive data on *P. sedentaria* were reviewed by K. H. Barnard (1932), who indicated that, in the more northern regions of its distribution, this species has its highest period of reproductive activity during the summer and fall months. Table 10 gives the breeding information gathered in this present study.

The peak of egg production occurred in the summer. Since the developing young of this species are carried for some time on the inner walls of the salp "barrels" in which *P. sedentaria* is known to live, and only a few of these "barrels" were collected, probably the percentages of females with young are inaccurate. Because of the confusion regarding the release of young from the parents (or from the barrels), it is difficult to analyze the size variations as related to breeding season. In addition to this problem, one can see from Table 10 that the extensions of the lower limits of the size range for males and females do not coincide. In spite of these difficulties, however, males were most prevalent during the times of high egg production and the other data do indicate greatest reproductive activity during the summer and fall months, concurring with Barnard's 1932 report.

## Family PARAPHRONIMIDAE

### *Paraphronima gracilus* Claus

A total of 472 specimens was collected from pint aliquots. Hurley (1956) reported a single female with young in the brood pouches during August. His work was conducted in the local southern California area near the collection sites of this present study.

As indicated in Table 11, the highest percentages of ovigerous females were noted in the fall and females carrying young were most

TABLE 10

SEASONAL VARIATION IN THE PERCENTAGES OF MATURE FEMALES CARRYING OVA (O) AND YOUNG (Y), THE MEAN SIZE OF FEMALES (MSf) AND MALES (MSm), SIZE RANGE OF FEMALES (SRf) AND MALES (SRm), THE FEMALE/MALE RATIO (f/m), AND THE AVERAGE NUMBER PER TRAWL HOUR (n/th) FOR *Phronima sedentaria*

| SEASON | O | Y | MSf (mm) | MSm (mm) | SRf (mm) | SRm (mm) | f/m | n/th |
|---|---|---|---|---|---|---|---|---|
| Summer | 53% | 20% | 25 | 16 | 11–35 | 11–17 | 2.4/1 | 20 |
| Fall | 20% | 3% | 22 | 14 | 14–33 | 9–18.5 | 2.2/1 | 15 |
| Winter | 7% | 22% | 27 | 13 | 13–35 | 11–15 | 10/1 | 8 |
| Spring | 25% | 19% | 28 | none | 18–37 | none | no males | 3 |

TABLE 11

Seasonal Variation in the Percentages of Mature Females Carrying Ova (O) and Young (Y), Mean Size of Females (MSf) and Males (MSm), Size Range of Females (SRf) and Males (SRm), and the Average Number per Trawl Hour (n/th) for *Paraphronima gracilus*

| season | O | Y | MSf(mm) | MSm(mm) | SRf(mm) | SRm(mm) | n/th |
|---|---|---|---|---|---|---|---|
| Summer | 8% | 50% | 13.5 | 10.5 | 9–16.5 | 10–14 | 8 |
| Fall | 43% | 47% | 10 | 10.5 | 9.5–13 | 10–11 | 33 |
| Winter | 24% | 55% | 11 | 10.5 | 10–12 | 10–11 | 18 |
| Spring | 2% | 75% | 11 | 11 | 10–12 | 10–12 | 20 |

TABLE 12

Seasonal Variation in the Percentages of Mature Females Carrying Ova (O) and Young (Y), Mean Size of Females (MSf) and Males (MSm), Size Range of Females (SRf) and Males (SRm), and the Average Number per Trawl Hour (n/th) for *Paraphronima crassipes*

| season | O | Y | MSf(mm) | MSm(mm) | SRf(mm) | SRm(mm) | n/th |
|---|---|---|---|---|---|---|---|
| Summer | 7% | 50% | 20 | 16.5 | 14–28 | 13.5–23 | 16 |
| Fall | 49% | 49% | 19 | 18.5 | 13–26.5 | 14–23 | 40 |
| Winter | 24% | 56% | 22 | 20 | 20–28 | 18–22 | 52 |
| Spring | 2% | 75% | 24 | 18.5 | 13.5–31 | 13–24 | 41 |

abundant in the summer. The female/male ratio was relatively low at the suggested time of ova production (2/1), and there was an increase in the average number per trawl hour from 8 per trawl hour in the summer to 33 per trawl hour in the fall, indicating the release of young into the mature population. There was also a drop in the mean size of the female population during the fall, but other size data offer no correlations.

*Paraphronima crassipes* Claus

A total of 922 individuals were recovered from pint aliquots. Hurley (1956) reported specimens collected in local waters during July and August to be carrying ova or young in their brood pouches. Table 12 gives the reproductive information regarding *P. crassipes* gathered in this present study.

The highest percentage of females with ova was noted in the fall, followed by a high incidence of young in the brood pouches in the winter and spring. Apparently young were released from most of the females in the summer and fall, during which time there was a drop in mean size and, by fall, an increase in the population density. The ratio of females/males was lowest during the fall (1/1), corresponding with the production of eggs.

## CONCLUSIONS

During this study certain general trends were noted regarding the reproductive activity of the total amphipod population. As illustrated in Table 13, the highest production of ova occurred during the summer and fall months, with development of young continuing throughout the following spring and summer. Most species released their young into the adult population by early fall, as indicated by the percentages listed in Table 13 along with the increase in the total amphipod population density.

It can be seen that, although the above mentioned trends are observed, precise analyses of the activities of individual species are complex and difficult to make. A sampling program de-

TABLE 13

Seasonal Variation in the Percentages of Mature Females with Ova (O) and Young (Y) in the Brood Pouches, and the Number per Trawl Hour (n/th) for the Total Amphipod Population

| season | O | Y | n/th |
|---|---|---|---|
| Summer | 24% | 40% | 49 |
| Fall | 20% | 32% | 135 |
| Winter | 10% | 35% | 50 |
| Spring | 14% | 43% | 40 |

signed specifically to obtain large numbers of individuals throughout the year is needed in order to eliminate density errors due to vertical migrations and gregarious activity. The fact that amphipods brood their young makes the group an ideal one for embryological studies if enough material can be obtained. The development and ecology of newborn amphipods could provide excellent problems for future research.

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